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HABITAT INDEX ANALYSIS OF THE HARBOR PORPOISE (*PHOCOENA PHOCOENA*) IN THE SOUTHERN COASTAL BAY OF FUNDY, CANADA

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ABSTRACT.—Boat transects were run through a variety of potential habitats of the harbor porpoise (*Phocoena phocoena*). Depth, topography, current speed, tidal amplitude, surface temperature, and lateness of season were considered in relation to mean sightings of harbor porpoises along each transect. Abundance of porpoises within the study areas was inversely correlated to mean August surface temperatures, possibly because a major prey species (Atlantic herring, *Clupea harengus*) was associated with vertically mixed waters. Abundance of porpoises was positively correlated both with physiographic features which concentrate herring in near-surface waters, and with increasing depth. The latter correlation may reflect the association of herring with deep water during daylight hours, as well as an aversion of porpoises to shallow, turbulent water. Equations based upon these correlations (adjusted $r^2 \geq 0.97$ at a scale of 1.0 km²) can be used to estimate the seasonal population density of harbor porpoises in areas of known depth, topography, and surface temperature.

Environmental effects upon the local distribution of the odontocete Cetacea are not well understood. Although relationships between abundance and factors such as topography (Evans, 1971; Hui, 1979), depth (Edel et al., in litt.), and temperature (Edel et al., in litt.; Fraker et al., 1979; Gaskin, 1968) have been detected, quantitative definition of such relationships is largely lacking.

Habitat index equations are mathematical expressions correlating abundance or species diversity to specific environmental characteristics (Johnson, 1975; Rosenzweig and Winakur, 1969; Smith and Gaskin, 1983). They provide insight into ecological relationships by defining such correlations, and are thus a practical first step towards understanding populations in the context of their environment. Habitat indices can also be used to estimate population density in an area with known environmental characteristics.

The only cetacean population to which habitat indices have been applied is *Phocoena phocoena*, the harbor porpoise, in the Deer Island area of the Bay of Fundy (Smith and Gaskin, 1983). That preliminary study emphasized mother/calf pairs, however, and was based upon unstandardized data not intended for such analysis. The application of index techniques to all social categories of harbor porpoises, over a broader geographic area, and using standardized data, builds and expands upon this initial work.

We used habitat index equations to examine several environmental factors potentially related to the local distribution of harbor porpoises in the coastal waters of the southern Bay of Fundy. This also represents the first attempt to derive sighting density equations suitable for estimating population.

METHODS

Three study areas in the southern coastal Bay of Fundy were sampled from 15 June to 1 September 1981 and 1982 (Fig. 1a). These included the Digby Gut/Annapolis Basin area, the northern and eastern edges of Grand Manan Island, and the archipelago to the north and east of Deer Island. Each area was sampled with equal emphasis throughout the summer.

In each area, a series of 5-km transects were run using small boats (4 m, observer height above water 2 m) through areas of differing depth, topography, and oceanographic activity (Fig. 1b, c, d). To maintain constant sighting efficiency, transects were surveyed only under conditions of unlimited visibility and estimated wave height <30 cm (Beaufort Sea State 0 or 1). Each survey of a transect was completed in 35–40

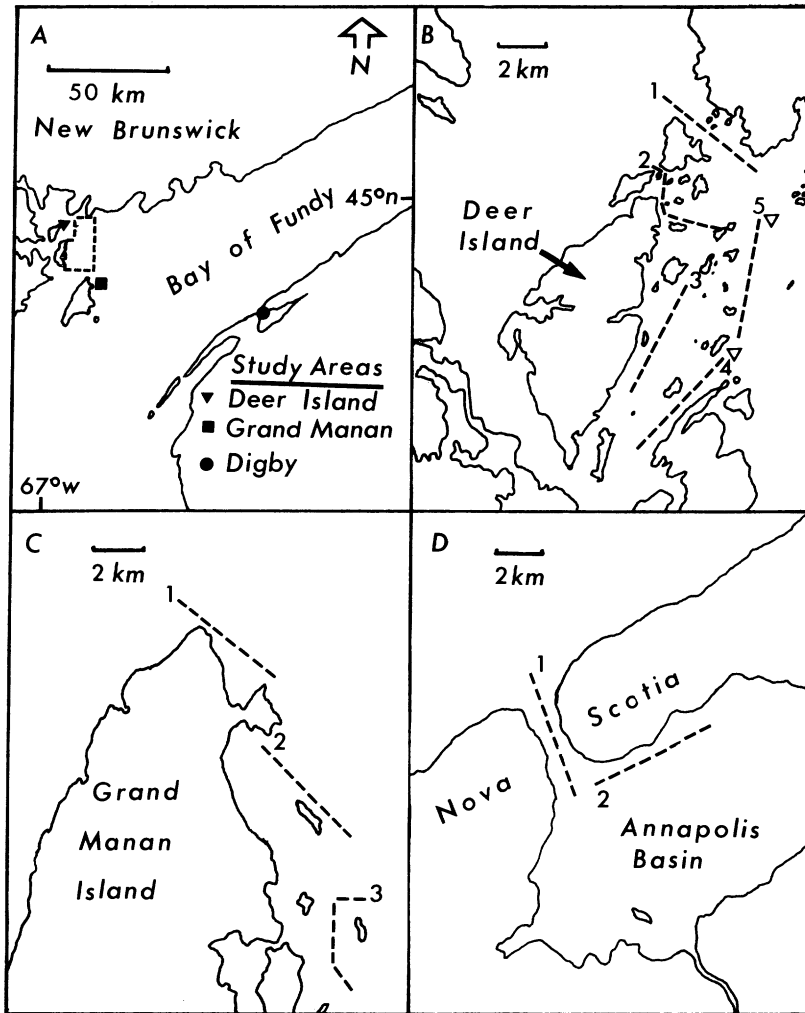


FIG. 1.—The study areas. 5-km transects are shown in b), c), and d) as dashed lines. Transect numbers are shown at segment 1 of each transect. a) The southern Bay of Fundy, showing the location of the three study areas. The Outer Quoddy area is enclosed by the dashed line. b) The Deer Island area. Open triangles denote localities at which $H = 1$. Transect 4 runs along Head Harbour Passage; transect 1 runs along Letite Passage. c) The Grand Manan area. d) The Digby area.

min, at an average speed of 8 km/h (2.2 m/s). Surveys whose durations fell outside these limits were discarded to maintain uniform sighting effort among replicates. Constant speed was assumed during runs. To assist in approaching this ideal, elapsed time to convenient landmarks was gauged against “ideal” times which assumed a transect duration of 37.5 min. As tidal currents in the Bay of Fundy are very swift (Forrester, 1958), transects were run against the current to control observer speed more easily.

Each transect was generally sampled at least 12 times per summer, except for those which yielded no more than one contact during 1981 (DE2, GM3, and DI2); these transects were only sampled six times during 1982. DE5, which was run only during 1982, was sampled 27 times during that year to maintain similar sample sizes. A series of unpaired t -tests applied to all other transects revealed no significant differences between 1981 and 1982 mean sightings/h ($t \leq 1.75$, $d.f.$ from 5 to 12, $P > 0.1$), permitting comparison of DE5 data with that of the other transects.

There was equal sampling emphasis on periods of flood, ebb, and slack tide. Furthermore, runs during slack tide were divided equally between high water and low water phases. To minimize dependence between replicates of the same tidal phase, surveys made during the same phase for any given transect were run on different days.

During runs, constant watch was maintained for harbor porpoises across the forward 180° of the transect path. Unaided-eye observation was adopted for the most part, and binoculars were used to sweep the search arc about twice every kilometer, and to determine the group size of contacts already made.

Estimated sighting angle (0° lying directly ahead along the transect line), range, and number of porpoises were recorded for each contact using a portable cassette tape recorder. Range estimates were made visually. Such estimates on stationary floating objects were accurate to ± 15 m at 100 m estimated range, using readings from a stereoscopic rangefinder as a standard. The rangefinder could not be used for ranging actual porpoise contacts due to the brief and intermittent nature of the sightings.

To avoid re-counting established contacts, the position of each new sighting was compared with those of previous contacts of similar composition. If a previous contact could have moved to the location of the new sighting in the time between sightings, the new sighting was not counted. This determination could usually be made in the field; however, in some cases the estimated positions of relevant sightings were plotted on nautical charts, after the survey. We believe that this procedure effectively minimized any upward bias in the counts (Hilby, 1982).

All remaining sightings were noted regardless of range. This permitted expression of the data only in relative terms of sightings/h, but allowed an index to be based upon the maximum available data. However, by plotting the frequency of sightings against perpendicular distance from the transect line, and by determining the distance beyond which sighting efficiency decreased, it was possible to derive a strip transect to be used as a basis for preliminary population estimates (Eberhardt, 1978). Frequency of sightings dropped by over half beyond a perpendicular distance of 25 m from the transect line; therefore the derived strip was 50 m wide.

Although logistic constraints necessitated the use of different boats in different study areas, and two observers were used rather than one in 20% of the runs, a series of simultaneously run comparative transects revealed no significant differences in sighting efficiency resulting from these changes ($t < 1.00$, $d.f. = 6$, $P > 0.1$).

Each transect was divided into five 1-km segments, each assumed to be environmentally homogeneous. Eight environmental variables were measured along each segment. The first four variables listed below remained constant throughout both field seasons and were not measured every run. The remaining variables were recorded separately during each survey.

Depth (m) at low water.—Depth was obtained for all areas from nautical and field charts (Canadian Hydrographic Service, 1981; National Oceanic and Atmospheric Administration, 1978); listed soundings within 100 m of the transect line were averaged throughout each segment.

Topography.—Topographic variability was measured using an index previously derived to assess this factor throughout the range of three species of Pacific dolphin (Hui, 1979), following the form:

$$C = ((D_{\max} - D_{\min})/D_{\max}) \times 100 \quad (1)$$

where D_{\max} and D_{\min} are maximum and minimum depths, respectively, of the area in question. This is a useful relative measure of maximum, not average, topographic variability. We used listed soundings up to 100 m from the transect line when calculating C .

Current speed at fast flood (m/s).—This was measured using drift drogues (with vanes extending to 1 m below the surface of the water) released within an hour of fast flood tide, when tidal amplitude was between 5.9 m and 6.2 m. Displacement during 10-minute intervals was determined by triangulation using landmarks.

Herring entry points (H).—This is a dummy variable based upon the two most probable entry routes of Atlantic herring (*Clupea harengus*) into the inshore waters of the Deer Island archipelago (the "Inner Quoddy" subarea). These are the approaches to Letite and Head Harbour passages (Graham, 1933; Iles, in litt., 1979; Jovellanos, 1981; McKenzie and Skud, 1958; McKenzie and Tibbo, 1961) (Fig. 1b). Such points are characterized by the shoreward penetration of deep (>80 m) channels flanked by relative shallows, and by the funneling of flood tidal currents through these channels. Essentially, they act as bottlenecks through which large volumes of water and their contents are transported during flood tide. No comparable mechanism for concentrating herring may exist anywhere else in the southern Bay of Fundy because up to 80% of historical weir catches in the Fundy region have occurred in the Quoddy area (Graham, 1933; Jovellanos, 1981). H equalled 1 for segments falling within 1 km of such a point (DE41, DE51, and DE55). H equalled

TABLE 1.—Summary statistics for Equations 2 to 6.

Statistic	Eq. 2	Eq. 3	Eq. 4	Eq. 5	Eq. 6
<i>R</i> ²	0.566	0.495	0.978	0.989	0.977
Adjusted <i>R</i> ²	0.557	0.485	0.972	0.984	0.965
<i>SE</i> of estimate	0.467	0.428	0.472	0.447	0.918
<i>F</i>	62.58	47.14	155.7	185.5	83.83
<i>n</i> *	50	50	10	10	10

* Each data point represents 18–27 replicates (see text for details).
NOTE: All equations are significant at *P* < 0.0001.

0 for all other segments. When analysis involved the entire transect, *H* equalled 1 for an entire transect if at least one of its segments lay within 1 km of a postulated entry point (DE4, DE5).

Surface temperature (°C).—Temperatures were taken to the nearest 0.5°C using a mercury thermometer.

Tidal amplitude (m).—Amplitudes were taken from appropriate tidal tables (Fisheries and Oceans, Canada, 1981, 1982).

Period in tidal cycle.—This was defined as the number of minutes after low water that each run began; it was calculated retrospectively from predicted low water (Fisheries and Oceans, Canada, 1981, 1982) and recorded starting times.

Seasonal day.—A measure of lateness of season, this was the number of days elapsed since 15 June of the appropriate year.

Upwelling, rip, and boat activity were also noted in general terms during each pass through a segment.

Data for each segment within a given transect were considered independently. Data from all segments within each transect were also pooled to produce mean environmental and sighting values applicable to the transect as a whole. Analysis was therefore possible at two spatial scales, that of an individual segment and that of an entire transect. Furthermore, results at each scale could be expressed either as sightings/h (using the entire sighting data base) or as sightings/km² (using only those sightings made within the 50 m strip). Multiple regression analysis was applied in all four cases, using BMDP packages P1r (Multiple Linear Regression), P4r (Principal Components Regression), and P9r (All Possible Subsets Regression) (Dixon et al., 1981). The options provided in these programs permitted testing for, and correction of, any significant non-normality, multicollinearity, inconstant variance, or bias in the data.

RESULTS

During this study, a total of 415 porpoises were sighted in 339 groups during approximately 154 hours of observation. None of the environmental variables considered were significantly correlated with the results of individual surveys (*P* > 0.1). Further analysis was therefore concerned with mean sightings of porpoises along each transect throughout the season. This precluded further analysis of any of the strictly time-dependent variables (tidal amplitude, period in tidal cycle, and seasonal day).

Of the remaining variables, only depth, *H*, and mean August surface temperatures were significantly correlated with mean sighting frequency (*P* < 0.1) (Table 2). Therefore, mean sightings/h (over both seasons) for each segment were regressed against these three variables and their various interactions. At the segment scale, the small-scale movements of individual porpoises produced high levels of sighting variance. Dependent variables were log-transformed to counter this and to normalize the data. The optimum resulting equations are of the form:

$$\log(Y_1 + 0.1) = 0.019D - 0.772 \tag{2}$$

and

$$\log(Y_2 + 0.1) = 0.015D - 0.897, \tag{3}$$

where *Y*₁ = mean sightings/hour, *Y*₂ = mean sightings/km², and *D* = depth (Fig. 2). Both equations are highly significant (*P* < 0.0001), but have low *R*²s (Table 1).

Most of the fit of Equations 2 and 3 is due to the depth component, *D* (Table 2). The estimates generated by both equations increased exponentially with depth, producing unrealistically high

TABLE 2.—Summary statistics for components of Equations 2 to 6.

Component and statistic	Eq. 2	Eq. 3	Eq. 4	Eq. 5	Eq. 6
<i>D:</i>					
Regression coefficient	0.019	0.015	0.045	0.027	0.022
±SE of coefficient	0.002	0.002	0.009	0.009	0.018
<i>P</i>	<0.001	<0.001	0.002	0.018	0.263
Contribution to <i>R</i> ²	0.566	0.495	0.079	0.018	0.006
<i>H:</i>					
Regression coefficient			4.10	6.34	9.72
±SE of coefficient			0.577	0.563	1.16
<i>P</i>			<0.001	<0.001	<0.001
Contribution to <i>R</i> ²			0.159	0.226	0.274
<i>T:</i>					
Regression coefficient				−0.397	−0.503
±SE of coefficient				0.185	0.380
<i>P</i>				0.076	0.234
Contribution to <i>R</i> ²				0.008	0.007

estimates of abundance in deep water (716 sightings/h and 20 sightings/km² at 200 m depth) (Fig. 4). This was due to the logarithmic transformation of the dependent variables in Equations 2 and 3, which in effect converted the dependent variables into powers of ten.

The mean sighting and environmental values from the segments within each transect were then averaged to produce mean values applicable to each transect as a whole. The movement of individual animals was less significant at this larger spatial scale, and the dependent variables could be regressed without transformation. The resulting equations took the form:

$$Y_1 = 0.0447D + 4.10H - 0.159 \quad (4)$$

and

$$Y_2 = 0.277D + 6.34H - 0.397T + 5.00, \quad (5)$$

where *H* = herring entry points and *T* = mean August surface temperature. The predicted increase in sightings with increasing depth, although still the strongest relationship, was much less dramatic than was the case for Equations 2 and 3 (Fig. 4). Both equations were highly significant (*P* < 0.0001), and had very high *R*²s (Table 1).

Equations 4 and 5 were sufficiently reliable (see Draper and Smith, 1981) to predict mean summer sightings of harbor porpoises within the study areas. Equation 5 produced an estimate of mean summer population density; it was probably conservative since the intermittent visibility of the subjects (and consequent imperfect sighting efficiency) should downwardly bias the estimates. All points within the transect strip came within 60 m of the observer for periods equalling or exceeding the mean submergence time of a nondiving harbor porpoise (15–25 s; Read, 1983; Watson and Gaskin, 1983) (Fig. 5). Assuming a random distribution of porpoises within the strip, this suggested that most if not all of the nondiving porpoises present in the strip surfaced at least once while within effective sighting range. However, diving porpoises (mean submergence time 1.44 min; Watson and Gaskin, 1983) could easily have escaped detection under these conditions. Since we did not know what proportion of the animals were diving at any given moment, we were unable to realistically correct for any resulting conservatism.

As a test of the predictive value of habitat index techniques, a further equation was based solely upon data collected from 15 July to 31 August, when harbor porpoises were most abundant in the Fundy region (Gaskin, 1977; Neave and Wright, 1968; Read, 1983). This equation,

$$Y_2 = 0.0219D + 9.72H - 0.503T + 6.79 \quad (6)$$

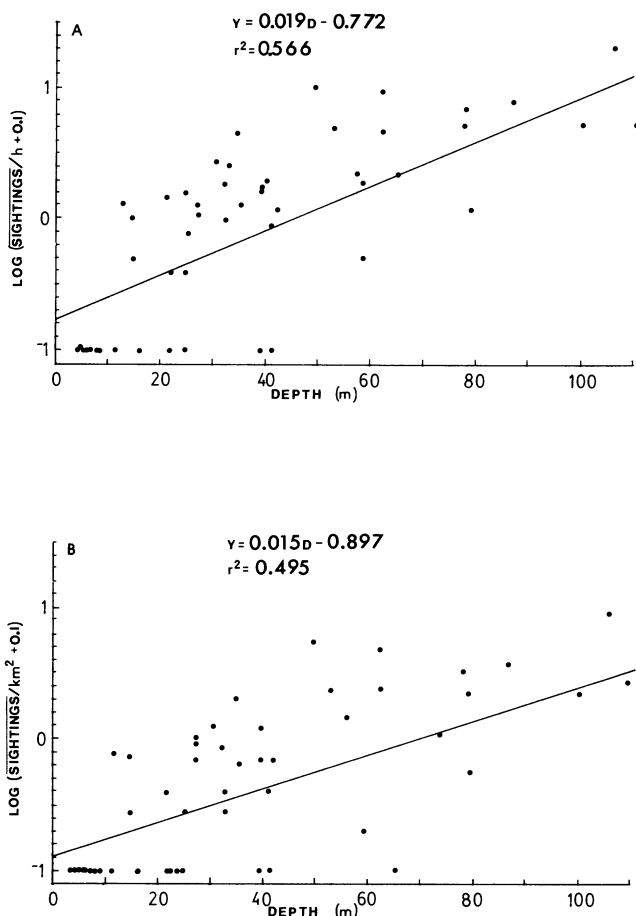


FIG. 2.—Habitat index equations for harbor porpoises at the segment scale, using A) mean sightings/h and B) mean sightings/km² as the dependent variable.

was significant at $P < 0.0001$ (Table 1), although the exclusion of data gathered prior to 15 July greatly reduced the significance of the depth and temperature components (Table 2).

By excluding data from the early part of the summer, we could compare our results with those of shipboard porpoise surveys undertaken in the Outer Quoddy area during late July and August (Gaskin et al., in litt.). The Outer Quoddy area lies between the Deer Island and Grand Manan study areas, but does not overlap with either (Fig. 1a). It has a mean depth of 82.7 m (Canadian Hydrographic Service, 1981), and had a mean August surface temperature of 11.6°C in 1981/82 (L. Murison, Zoology Dept., Univ. of Guelph, pers. comm.). Equation 6, using these values, produced an estimate of 2.8 porpoises/km², or 1,022 porpoises throughout the entire Outer Quoddy area (365 km²). Extensive shipboard censusing of the same area produced population estimates of 1,018 in 1981, 1,102 in 1982, and 1,270 in 1983 (Gaskin et al., in litt.).

DISCUSSION

Small-bodied (40–60 kg; Gaskin et al., 1974) inhabitants of cold water (Gaskin et al., 1974; van Bree et al., 1977), harbor porpoises are metabolically active animals (Kanwisher and Sundnes, 1965; Karandeeva et al., 1973) which eat up to 10% of their weight every day (Sergeant, 1969). Particularly in the Bay of Fundy, they feed largely upon Atlantic herring *Clupea harengus*

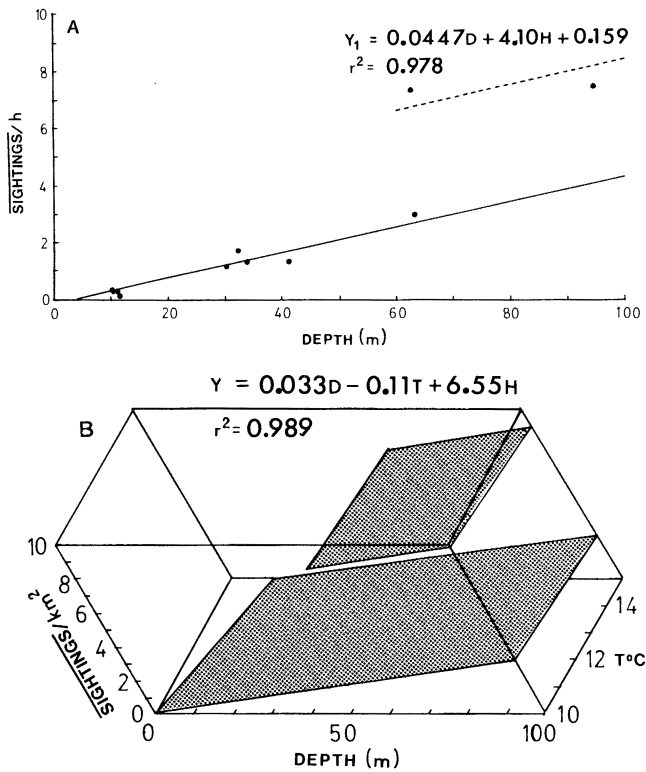


FIG. 3.—Habitat index equations for harbor porpoises at the transect scale, using A) mean sightings/h and B) mean sightings/km² as the dependent variable.

(Smith and Gaskin, 1974), an unpredictable food source (Graham, 1933; Jovellanos, 1981). These factors may act to restrict *P. phocoena* to areas of maximal prey availability, resulting in a narrow and readily-defined range of habitats relative to other coastal Odontocetes (Edel et al., in litt.). This is consistent with the high significance of Equations 2–6.

Equation 6 also illustrated the utility of habitat index analysis as an alternative to more conventional census techniques. The population estimate for the Outer Quoddy area generated by it agreed very well with estimates derived by shipboard surveys of that area, although it was based upon data from elsewhere in the Bay of Fundy.

The most distinct trend defined by Equations 2 to 6 was the increase in the abundance of harbor porpoises with increasing depth (Figs. 2, 3). An apparent preference for relatively deep water by harbor porpoises has been mentioned by Huber et al. (1982), and has been more convincingly demonstrated for mother/calf pairs of this species (Smith and Gaskin, 1983). The present study documented this relationship for harbor porpoises in waters up to 100 m deep in the southern coastal Bay of Fundy. However, the trend cannot continue indefinitely since the summer range of the harbor porpoise in the northwest North Atlantic lies mostly within the 200 m depth contour (Winn, in litt.; Winn and Edel, in litt.).

We suspect that the association of Fundy harbor porpoises with deeper water is at least partly related to prey availability. Atlantic herring generally feed near the surface of the water column at night and prefer depths of 20–500 m during the day, depending upon local depth restrictions (Blaxter and Holliday, 1963; Brawn, 1960). Head Harbour Passage, in the Deer Island area, was a significant exception (Battle et al., 1936) (see below). Since the data were collected during daylight hours, herring were presumably most abundant in deep, offshore water whenever

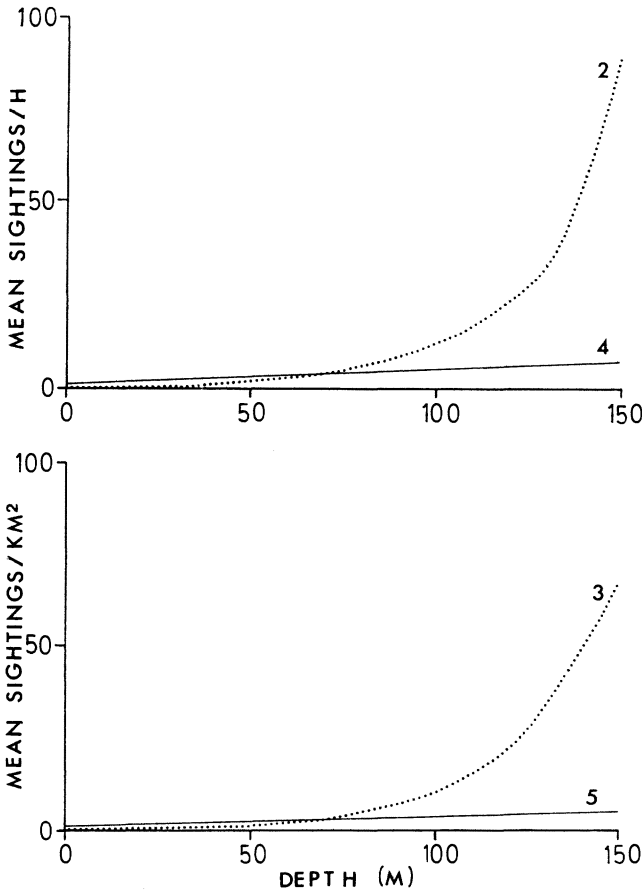


FIG. 4.—Harbor porpoise sighting estimates generated by Equations 2–5 across a range of depths, given that surface temperature is 10.0°C and $H = 0$.

transects were run. At such times, porpoises would presumably also be found in deep water, remaining close to their food supply.

Harbor porpoises have been routinely observed at depths of less than 10 m in Denmark (Amundin and Amundin, 1974), and have been reported “in fair numbers” in the shallow St. Croix Estuary (maximum depth 35 m, National Oceanic and Atmospheric Administration, 1978; Sergeant and Fisher, 1957). However, we sighted virtually no porpoises in water less than 10 m deep during the course of this study. This suggests that, in addition to any preference for deep water, porpoises in the Bay of Fundy may actively avoid shallow water. This may be due to the turbulence associated with shallow water throughout much of the study areas. In the southern Bay of Fundy, tidal currents can approach a maximum of 2 m/sec (Forrester, 1958). The present data indicated that stronger currents often occurred in relatively shallow channels which restricted the passage of water masses from deeper, less enclosed areas. Transect DE4 was a good example (Fig. 6). There was a dramatic decline in the mean number of porpoises sighted from segment 1 to segment 5; this was associated with decreasing depth, and increasing current speed and topographic variability. Since there was no apparent advantage in remaining in turbulent water, and since such behaviour would be energetically expensive, porpoises probably find it easier to avoid shallow (hence, turbulent) localities.

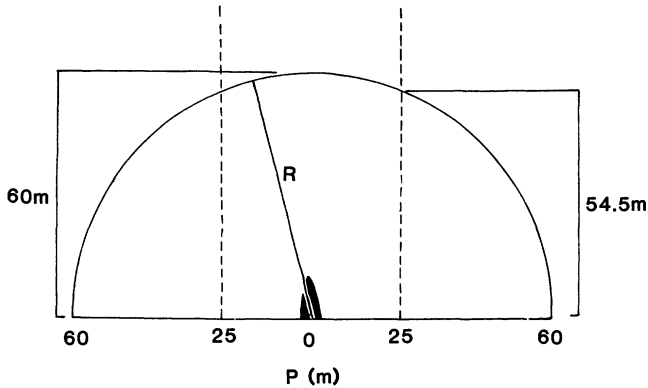


FIG. 5.—Schematic view of an observer moving at 2.2 m/s along the center of a 50 m-wide strip transect (boundaries denoted by dashed lines). The observer is at the base of a 180° search arc 60 m in radius. Perpendicular ranges from the center of the strip (P) are denoted along the base of the search arc. Stationary points remain within the radius of the arc (R) for time in sec (T) such that $T = (R^2 - P^2)^{0.5} / (2.2 \text{ m/s})$. Points along the center of the strip remain within the search area for 27 s, and those along the edge for 25 s.

Mean August surface temperature and mean sightings of porpoises were significantly and negatively correlated in Equation 5 (Table 2). Despite this, it is doubtful that slight temperature differences directly affect porpoise distribution. Porpoises enter the Bay of Fundy in large numbers when the surface water temperature rises above 7 or 8°C (Gaskin, 1977; Sergeant, 1978), and some are even known to overwinter in coastal waters (Gaskin, 1977). Temperatures recorded during the course of this study rarely fell below 9.0°C.

However, our present results, together with an apparent preference of porpoises for cold upwellings in the North Pacific (Huber et al., 1982), suggest a relationship to thermal stratification. Vertical mixing of the water column reduces surface temperatures (Sverdrup et al., 1942). Herring are associated with such mixing because of zooplankton concentration along convergence zones (Battle et al., 1936) and possibly due to transport of herring into surface waters by strong upwelling (Watson, 1976). Since the surface temperature of relatively unmixed areas increases throughout the summer, the association of herring with low surface temperatures would be most pronounced in late summer. Consequent correlation of porpoise sightings with temperature would also be most evident at this time. Smith and Gaskin (1983) have reported a similar correlation between sightings of harbor porpoises and September surface temperatures; however, we collected no data after August.

There was no significant T component in either of the equations expressed as sightings/hour (2 and 4). Since these were based upon all contacts regardless of range, they applied to a greater area than did equations based only on contacts made within the 50 m strip. Temperatures within the larger area would be more variable, and measurements taken along the transect line would thus be less representative, weakening the correlation.

It appears likely that both the depth and temperature components of Equations 3–6 were related to prey availability. The remaining component, H , presumably expresses this factor most directly. However, even H did not measure herring abundance at all, but rather the presence or absence of certain physiographic features. For example, along Head Harbour Passage, $H = 1$ only in segment 1. However, herring concentrated there are probably carried along the entire channel on their way to the Inner Quoddy subarea. For this reason H was not significant in Equations 2 and 3, which were based upon data from individual segments (Table 2). However, it was highly significant in Equations 4–6, which had lower resolution and allowed H to exert effects within broader spatial limits.

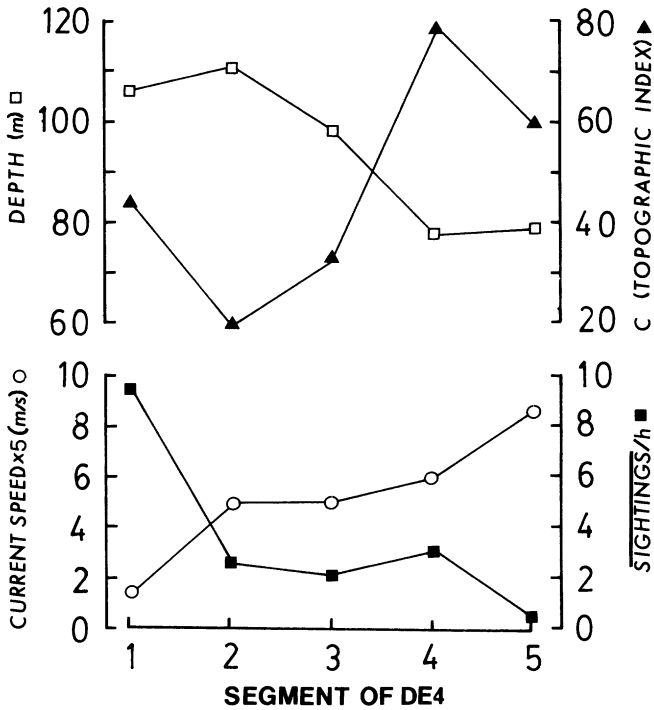


FIG. 6.—Depth, topography, current speed at fast flood $\times 5$, and mean hourly sightings of harbor porpoises along transect Deer Island 4. Topography is represented by (change in depth/maximum depth) $\times 100$ (Hui, 1979).

Admittedly, a dummy variable hardly constitutes a definitive measure of prey availability. It is however more useful than weir catch statistics, or even the use of computer models (Jovellanos and Gaskin, 1983) at their present stage of refinement; it is also much less expensive than would be intensive echosounding surveys of the study area. Despite its limitations, H is strongly correlated with sightings of harbor porpoises and is an indispensable component of Equations 4–6. Habitat equations which excluded it had high levels of bias (Mallows' $C_p \geq 40$ at the whole-transect scale).

The mouth of Head Harbour Passage (mean sightings/h = 20.2) yielded over twice as many porpoise sightings than did the mouth of Letite Passage (mean sightings/h = 7.8). However, $H = 1$ at both localities, and herring size classes at both entry points fell well within the 7.5–20 cm range (Graham, 1933; Jovellanos, 1981) taken by feeding harbor porpoise (Smith and Gaskin, 1974). This difference in porpoise distribution may be due to topographic differences between Head Harbour Passage and Letite approach. Incoming currents encounter immediate resistance from island masses and shoals along Head Harbour Passage. This results in stronger and more widespread upwelling than is caused by the gentler slopes of Letite (Graham, 1933; Watts, 1983). Due to this mixing, the near-surface waters of Head Harbour Passage contain significant quantities of deep-water plankton which are fed upon by herring (Battle et al., 1936). It is also possible that the herring themselves are carried into near-surface waters by topographic upwelling, since peak tidal currents in the region move faster (Forrester, 1958) than juvenile herring are able to swim for prolonged periods (Boyar, 1961). Finally, the presence of many nearby land masses would tend to keep herring concentrated in the passage itself. These factors should make herring in Head Harbour Passage much more accessible to feeding porpoises than those along the Letite approach, although the variable H cannot define this difference.

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